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THE CARPUS AND TARSUS OF THE EARLY PERMIAN SYNAPSID *SPHENACODON FEROX* (EUPELYCOSAURIA: SPHENACODONTIDAE)

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Abstract—The carpus and tarsus of the sphenacodontid synapsid *Sphenacodon ferox* are described in detail for the first time on the basis of nearly complete, loosely articulated examples from an incomplete, partially articulated skeleton from the Lower Permian El Cobre Canyon Formation of the Cutler Group of north-central New Mexico. On the one hand, the carpus and tarsus of *S. ferox* are compared to those of the more derived *Dimetrodon* and only member of Sphenacodontidae in which these structures are otherwise known adequately, and, on the other, to *Haptodus*, the sole member of the sister taxon of Sphenacodontoidea (Sphenacodontidae plus Therapsida). In order to recognize possible morphological trends in the carpus and tarsus within the combined clades of *Haptodus* and Sphenacodontidae, members of the sister clades Ophiacodontidae and Varanopseidae are utilized for outgroup comparison.

INTRODUCTION

The Late Pennsylvanian to Early Permian pelycosaurian-grade or basal synapsid amniotes include seven genera of Sphenacodontidae, some of which became a common component of Early Permian assemblages as the top predators. Knowledge of the carpus and tarsus of sphenacodontids is limited, however, to several species of *Dimetrodon*. For the carpus this includes *D. milleri, D. natalis, D. incisivus,* and *D. grandis* (Case, 1904; Gilmore, 1919; Romer and Price, 1940) and for the tarsus *D. milleri, D. natalis*, and *D. teutonis* (Romer and Price, 1940; Berman et al., 2004).

An incomplete, partially articulated skeleton of the sphenacodontid *Sphenacodon ferox* was recently collected from the Lower Permian interval of the El Cobre Canyon Formation of the Cutler Group of north-central New Mexico that includes the carpus and tarsus (Figures 1-2). Both are well preserved, loosely articulated, and complete except that the former lacks a small portion of the distal carpal series. This allows for the first time a description and reconstruction of both structures in *Sphenacodon*, as well as comparisons with those of the closely related *Dimetrodon* and other pelycosaurian-grade synapsids. Such comparisons provide the opportunity to recognize morphological trends in the carpus and tarsus of certain basal synapsid lineages.

MATERIALS

Sphenacodon ferox specimen CM 76895, the subject of this report, was discovered in an overbank deposit at the Cardillo Quarry (CM locality 998; Berman, 1993) in the Lower Permian interval of the El Cobre Canyon Formation near the village of Arroyo del Agua, Rio Arriba County, north-central New Mexico, during a joint field party of CMNH and NMMNH in 2002 (Zeigler et al., 2003a,b; 2005). CM 76895 consists of an incomplete, partially articulated skeleton, including an incomplete skull, that was collected in close association with two other basal synapsids: an incomplete, partially articulated skeleton, including some disassociated lower jaw elements, of the ophiacodontid *Ophiacodon* (CM 76896) and a few closely associated cranial elements of a varanopseid (CM 76897). Several features of *S. ferox* CM 76895 indicate an advanced stage of maturity, including complete ossification of the carpals and tarsals, and articular surfaces and processes of the limb elements. Smaller overall size, more slender build, and lesser-developed neural spines are features that distinguish *S. ferox* from the only other well-known species of *Sphenacodon*, *S. ferocior*, also from the Lower Permian of New Mexico (Romer and Price, 1940; Eberth, 1985).

Weight of the matrix-encased specimens and the remoteness of the Cardillo Quarry necessitated that the three specimens be removed as two plaster-jacketed blocks. Fortunately, the division appears to have isolated the *Sphenacodon* and *Ophiacodon* specimens from one another. Both the upper and lower surfaces of the block containing the *Sphenacodon* specimen were prepared, because it was not preserved in a single plane. Rather, the disarticulated portions of the partial skeleton were randomly scattered throughout the thickness of the block, but most importantly with the right forelimb and partial manus and the left pelvis, hindlimb, and partial pes preserved as articulated segments on the lower surface of the block. To facilitate preparation and study the carpus and tarsus were first isolated from the rest of the specimen and then imbedded in carbowax. After preparation in one view, the carpus and tarsus were re-embedded in carbowax and prepared in the opposite view. As a final stage, all but a few of the carpals and tarsals were completely isolated and were rearranged so as to depict their presumed correct positions and contacts with each other.

DESCRIPTION

Carpus

Ten of the expected eleven carpal bones are preserved in the right carpus of CM 76895, including the radiale, intermedium, ulnare, medial and lateral centrales, distal carpals 1-4, and pisiform (Fig. 1A). Whereas some of the carpals are narrowly disarticulated, most are preserved in close articulation, and only the approximately medial two-thirds of the fourth and the entire fifth distal carpal are missing, which were lost during collection of the specimen. In the reconstruction of Figures1B-C only the pisiform could not be repositioned, as it is attached to the ventral surface of the ulnare so that only half of its dorsal surface is exposed. Unless stated otherwise the carpus and tarsus are described as if viewed in dorsal aspect and in a single plane.

The radiale is considerably thicker dorsoventrally than any of the other carpal bones, more so proximally, and has a pentagonal outline. The slightly concave, parallel medial and lateral margins are mostly free of contacts with other elements, though the latter seems to have had a narrow contact with the intermedium. The proximal articular surface for the radius is flat, semicircular in outline with a convex dorsal and a straight ventral margin, and deepens toward the lateral margin of the bone. Distally, the radiale is wedge-shaped with each side of

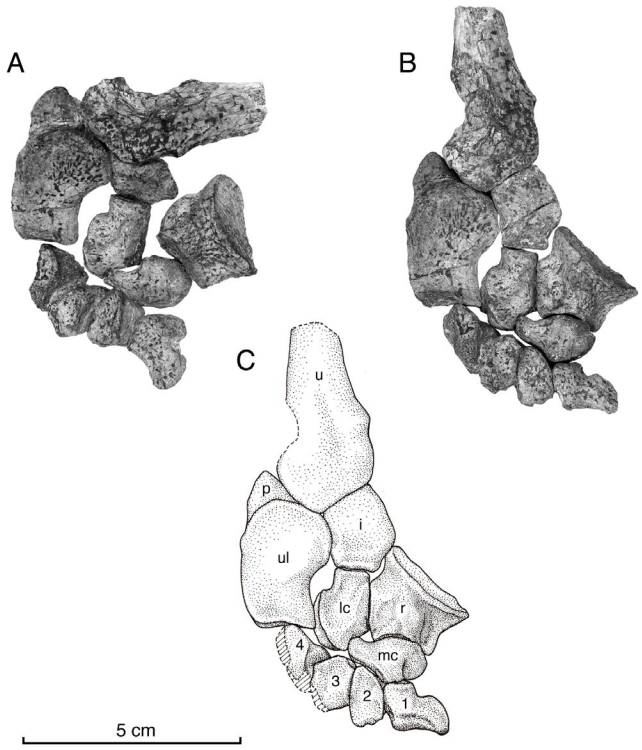

FIGURE 1. Carpus of *Sphenacodon ferox*, CM 76895. A, Photograph of specimen as preserved; B, photograph of carpal elements rearticulated into presumed correct position; C, drawing of B. Note that pisiform and distal carpals 3 and 4 were not separated from one another and repositioned in reconstruction of B and C. Abbreviations: i, intermedium; lc, lateral centrale; mc, medial centrale; p, pisiform; r, radiale; u, ulna; ul, ulnare; 1-4, distal carpals 1-4.

the wedge being occupied by large articular surfaces, one facing distomedially and the other distolaterally for the medial and lateral centrales, respectively. Both facets are ovate in outline, deepen slightly as they converge distally, and differ only in that the facet for the medial centrale is broadly concave, whereas that for the lateral centrale is flat. Distally, the two articular surfaces are separated along at least the dorsal half of the distal edge of the wedge by a very narrow channel of smoothly finished bone. A well-developed, broadly rounded ridge extends across the dorsal surface of the radiale between the summits of the distomedial and proximal articular surfaces, whereas the ventral surface of the radiale is deeply concave. The intermedium is the only carpal element whose correct position was preserved markedly altered, having been rotated dorsodistally about its distal end so that its dorsal surface faces distally. It is pentagonal in outline with proximal and distal surfaces occupied entirely by flat, transversely elongate, oval articular surfaces that contacted the ulna and lateral centrale, respectively. All but a small distal portion of its very slightly concave lateral margin contacted the ulnare, leaving the small, distal portion of the margin to contribute to the medial border of the large opening for the perforating artery. Relative to the other carpal bones the intermedium is very thin dorsoventrally, with a rather flat dorsal surface and a ventral surface that is broadly concave in proximodistal section due to pronounced, ventral thickenings to accommodate the proximal and distal articular surfaces.

The proximodistally elongate ulnare is the largest carpal element. The proximal half of the ulnare is flat and flared medially with a broadly convex articular margin. Its medial contact with the intermedium produces a slightly greater-than-right angle union between their proximal articular surfaces that received the ulna. The lateralmost portion of the proximal articular surface of the ulnare received the pisiform. The distal half of the ulnare is slightly convex in transverse section and rectangular in outline and ends distally in a transverse, flat articular surface that has a laterally deepening, ovate outline with a slightly concave ventral margin. This surface apposes the fourth distal carpal and presumably also narrowly the fifth distal carpal. The free, convex union between the medially flared proximal and the proximal half of the rectangular distal portion of the ulnare form the lateral border of the large, oval opening for the perforating artery. In apparent contrast to other basal synapsids, the distal end of the ulnare is not noticeably expanded medially into a footplate, nor does the bone at this level of its medial margin curve ventromedially to form a thin, flange-like structure that contacts the lateral centrale. Rather, the medial margin of the distal portion of the ulnare has a strongly convex surface in transverse section that deepens ventrally as it extends a short distance onto the ventral surface to form a condyle-like facet that apparently contacted the lateral centrale. This structure produces a deep, proximodistal channel on the ventral surface of the distal portion of the ulnare. A large pisiform partially underlies the lateralmost portion of the convex proximal end of the ulnare at or very near the presumed site of their articulation. Exposure of the ventral surface of the pisiform reveals an elongate oval outline, and presumably its long axis was directed approximately proximolaterally so that the pisiform narrowly contacted the ulnare.

In general, the medial centrale has a transversely ovate outline, but with the lateral half constricted by broadly concave proximal and distal margins to produce a narrow, process-like structure. The convex proximal margin of the medial portion bears a large, rounded, articular surface for the radiale. The distal end of the narrower lateral portion contacted the distalmost end of the lateral margin of the lateral centrale, leaving most of its concave proximal margin, which is finished in smooth bone, free of contact. The distal margin of the medial centrale contacted the first three distal tarsals, with the convex margin of the medial portion contacting the first distal carpal and the concave margin of the lateral portion contacting the second and third distal carpals. A broadly rounded swelling extends proximodistally across the medial portion of the medial centrale. There is no indication of a large sesamoid bone that Gilmore (1919) theorized articulated with the medial edge of the medial centrale in *Dimetrodon grandis*. Nor is there evidence that a small medial sesamoid may have been present close to the junction of the medial centrale and radiale as suggested by Romer and Price (1940) in other pelycosaurian-grade synapsids.

The stout, proximodistal oblong lateral centrale occupies a central position in the carpus and contacts all of the bones immediately surrounding it. A flat, transversely oval articular surface occupies the proximal margin and contacts the intermedium. Its width is narrowed laterally by a small, right-angled notch that forms, together with a short distance of the lateral margin distal to it, the greater distal portion of the medial border of the large opening for the perforating artery. A short distance beyond the opening for the perforating artery the lateral margin of the lateral centrale is continued by a deep, channel-like articular surface that undoubtedly contacted the condyle-like facet of the ventromedial margin of the distal portion of the ulnare. The greater proximal portion of the medial margin of the lateral centrale is straight and occupied by a large, flat articular surface that is inclined slightly onto the dorsal surface of the bone in a broadly convex margin and contacted the distolateral margin of the wedge-shaped distal end of the radiale. Distally the lateral centrale ends in a small, triangular portion that extends a short distance beyond the level of the distal margins of the radiale and ulnare. Its slightly concave medial margin is contacted by the narrow lateral end of the medial centrale, whereas a deep articular surface on its convex lateral margin contacts the third and fourth distal tarsals.

Distal carpals 1-4 are preserved, although the third is missing a small portion of its distolateral margin and the fourth is incomplete laterally. With one exception they occupy nearly their proper relationships with each other and the more proximal elements of the carpus,

with closely apposing, essentially flat, well-developed, vertical articular surfaces. The fourth, however, which could not be separated from the third distal carpal, remains slightly dislocated from its contact with the lateral centrale in the reconstructed carpus of Figures 1B-C. The first distal carpal greatly exceeds the others of the series in its transverse width. This feature is expressed by the greatly expanded, transverse width of its concave distal articular surface that faces distoventrally for the equally expanded proximal end of the first metacarpal. It has a roughly L-shaped outline, with a deep, semicircular notch forming the internal angle between the shorter vertical arm and the longer, medially directed horizontal arm. The free proximal and medial margins of the horizontal arm form a broadly convex margin. A narrow, abrupt, step-like depression of the dorsal surface bordering the distal concave margin gives the dorsal surface its slightly convex appearance in proximodistal section. Articular surfaces of the proximal and lateral margins of the vertical arm contact the medial centrale and second distal carpal, respectively. The second distal carpal has an ovate dorsal outline, narrowing proximally along its long axis, with the proximal half of its medial margin contacting the medial centrale. As in distal carpals three and four, it has a concave dorsal surface of finished bone. The distal articular surface of distal carpal two, as well as those of three and four, has the outline of an inverted triangle with a slightly concave face in vertical section. The third distal tarsal is roughly pentagonal in dorsal outline, narrowing slightly proximally to a widely angular articular surface that contacts the complementary angular union between the distal marginal surfaces of the medial and lateral centrales. Although only a narrow portion of the medial side of the fourth distal carpal is present, it is obvious that the intact element would have had broad contacts with the distolateral margin of the lateral centrale and most of the distal margin of the ulnare.

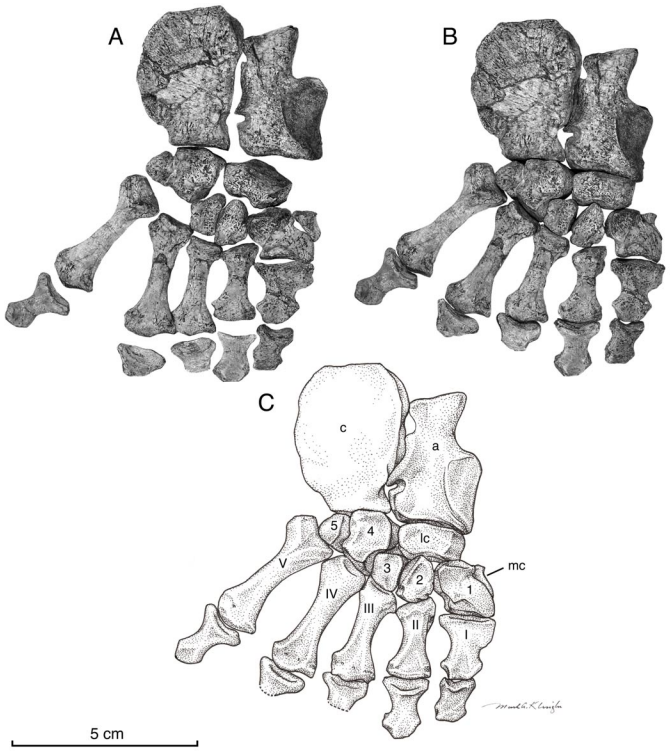

FIGURE 2. Partial pes of *Sphenacodon ferox*, CM 76895. A, Photograph of specimen as preserved; B, photograph of reconstructed specimen; C, drawing of B. Note that in B and C the medial centrale and the first distal tarsal and distal tarsals 4 and 5 were not separated from one another and repositioned. Abbreviations: a, astragalus; c, calcaneum; lc, lateral centrale; mc, medial centrale; 1-5, distal tarsals 1-5; I-V, metatarsals I-V.

Tarsus

The complete set of nine tarsal bones is preserved in CM 76895 (Fig. 2) that includes the astragalus, calcaneum, medial and lateral centrales, and distal tarsals 1-5, and their narrow separation to close articulation allows a reasonable interpretation of their original relationships to each other (Figures 2B-C). The large, stout astragalus has a sharply angled L-shaped outline, with the length of the vertical arm being nearly twice that of the horizontal arm when measured along the internal margins of their angular union. The dorsal surface of the astragalus is of smoothly finished bone and relatively flat except for where it is raises along the dorsal margins of the articular areas for the calcaneum, tibia, and lateral centrale. The apposing margins of the astragalus and calcaneum meet in a nearly straight contact that is interrupted at two places: 1) a small, transversely narrow, rectangular notch at the proximolateral corner of the astragalus, and 2) a well-developed foramen for the perforating artery near the distal end of their apposing margins. Between these two features the astragalus and calcaneum are joined by matching, well-developed, essentially flat, oval articular surfaces. Distal to the foramen for the perforating artery the contact is short, with the articular surface of the astragalus being slightly convex in transverse section and contacting a narrow, vertical channel on the calcaneum. The astragalus is much shorter proximally than the calcaneum, but both end distally at nearly the same transverse plane. The proximodistally sloping proximal margin of the astragalus and the convex proximomedial corner of the calcaneum form between them an abrupt, approximately right-angled margin whose articular surface for the fibula has an ovate outline that narrows markedly laterally. An especially prominent feature of the astragalus is a well-defined, transversely convex, condyle-like articular surface for the tibia that expands distally as it extends from the dorsal surface of the horizontal arm to the ventral edge of its medial margin. The distal margin of the astragalus is occupied by a transversely elongate, slightly concave articular surface that apposes the lateral centrale.

The calcaneum has in general a proximodistally elongate oval outline, thinning in thickness toward its free, convex proximal and lateral margins and thickening toward its straight medial and distal margins where its bears articular surfaces for the fibula and astragalus and the fourth and fifth distal tarsals, respectively. The transverse, distal articular margin for fourth and fifth distal tarsals is deep, essentially flat with an outline that is convex dorsally, straight ventrally, and narrows laterally.

The medial centrale, smallest of the tarsal elements, is preserved tightly cemented to the medial margin of the first distal tarsal, and no attempt was made to separate the two elements. As preserved, it is narrowly triangular in both dorsal outline and transverse section, broadening proximally toward an oval articular surface that is preserved free of contact. The original site of articulation of the medial centrale was probably at the proximal end of the medial margin of the first distal tarsal, where the proximal articular surface extends a short distance onto its medial margin. If the medial centrale articulated at this site, it would have projected presumably distally and slightly medially, paralleling the medial margin of the first distal tarsal. The stout, transversely broad, subrectangular lateral centrale has a strongly concave dorsal surface due to highly raised proximal and distal margins and a slightly raised medial margin that reflect well-developed marginal articular surfaces. The proximal margin is completely occupied by an articular surface for the astragalus that is mediolaterally oval and slightly convex in proximodistal section. The central area of its distal margin is emarginated slightly by a concave articular surface that only partially apposes the second distal tarsal, whereas on either side convex articular surfaces appose the first and third distal tarsals. The lateral margin of the lateral centrale is occupied by an essentially flat articulation surface for the fourth distal tarsal.

The distal tarsal series vary greatly in dorsal outline, have con-

cave dorsal surfaces of smoothly finished bone except for that of the first and fifth being slightly convex, and possess distal articular surfaces for their respective metatarsals that are slightly convex in proximodistal section and inclined slightly ventroproximally in the distal tarsals 1-3 and flat in distal tarsals four and five. The first distal tarsal is essentially identical to the first distal carpal. It is subequal in size to the fourth, with both being substantially larger than the others of the series, and has a roughly L-shaped outline, with a pronounced semicircular notch forming the internal angle between the shorter, wider, vertical arm and the longer, narrower, medially directed horizontal arm. The resemblance to the first distal carpal is further strengthened by the free proximal and medial margins of the horizontal arm forming a smoothly convex margin and the narrow, abrupt, step-like depression of the dorsal surface bordering its distal margin. The particularly wide, distal margin is occupied entirely by an articular surface that is matched in width by that of the greatly expanded head of the first metatarsal. The second distal tarsal has roughly the outline of a proximodistally elongate triangle with unequal sides and a proximal apex that contacts narrowly the lateral centrale. Its slightly concave medial and convex lateral margins accommodate articular surfaces for the first and third distal tarsals. The third distal tarsal is trapezoidal in outline, with its medial and lateral margins being parallel, and the former being the longest dimension of the bone and contacting the entire lateral margin of the second distal tarsal. Contact with the lateral centrale appears to be restricted to a narrow proximomedial corner, whereas its proximal and lateral margins meet in an obtuse-angled corner that fits snugly into a complementary notch in the distal half of the medial margin of the fourth distal tarsal. The fourth distal tarsal is pentagonal in dorsal outline, and its proximolateral corner appears to have had a narrow contact with the distolateral corner of the astragalus. On the other hand, its entire slightly concave lateral margin is united snugly with the fifth distal tarsal, which has roughly the outline of a spherical triangle. The entire metatarsal series is preserved and closely duplicates that in *Dimetrodon* in their relative width-length proportions. The first metatarsal is very broad proximally, which is reflected in its broad contact with the first distal tarsal. Metatarsals 2 – 4 increase in length serially, with the fifth being subequal to the fourth.

DISCUSSION

Knowledge of the carpus and tarsus of *Sphenacodon ferox* not only allows their comparison with those of other pelycosaurian-grade or basal synapsids, but an opportunity to recognize possible evolutionary trends of these structures within certain closely related members of that group. Together with *Sphenacodon*, Sphenacodontidae currently includes *Bathygnathus*, *Ctenospondylus*, *Ctenorhachis*, *Dimetrodon*, *Neosaurus*, and *Secodontosaurus* (Reisz, 1986; Hook and Hotten, 1991; Reisz et al., 1992). Prior to the discovery of the carpus and tarsus of *Sphenacodon ferox*, *Dimetrodon* was the only sphenacodontid in which both these structures were well known. The carpus and tarsus are known also in *Haptodus* (Currie, 1977, 1979, and references contained therein), which was recently reassigned (Reisz et al., 1992; Berman et al., 1995) from Sphenacodontidae (Romer and Price, 1940; Reisz, 1986) to the sole member of a sister taxon to Sphenacodontoidea, defined as the combined clades of Sphenacodontidae and Therapsida. In the most recent phylogenies of synapsids (Kemp, 1982; Reisz, 1986; Reisz et al., 1992; Berman et al., 1995) they are divided into the sister taxa Caseasauria and Eupelycosauria. The former, which is not relevant to the present discussion, includes the families Eothyrididae and Caseidae, whereas Eupelycosauria includes Varanopseidae, Ophiacodontidae, Edaphosauridae, Sphenacodontidae, *Haptodus*, and Therapsida. The most recent analysis of the relationships of Sphenacodontidae (Reisz et al., 1992), which included only well-known representatives, supported the hypothesis that *Dimetrodon*, *Ctenospondylus*, and *Secodontosaurus* share a more recent common ancestor with each other than any of them do with *Sphenacodon*. However, with regard to the topic at hand, the carpus and tarsus of sphenacodontids is known only in *Dimetrodon*. Varanopseidae and Ophiacodontidae are universally viewed as sister clades to *Haptodus* and Sphenacodontoidea (Reisz, 1986; Reisz et al., 1992; Berman et al., 1995). Edaphosauridae, although not regarded universally as a basal clade within the Eupelycosauria (Reisz et al., 1992), need not be considered here, as its carpus and tarsus are unknown.

Of immediate interest here is a comparison of the carpus and tarsus in *Sphenacodon ferox* with those in the more derived sphenacodontid *Dimetrodon* as well as *Haptodus*, the sister taxon of Sphenacodontoidea. However, in order to recognize possible morphological trends in the carpus and tarsus within the combined clades of *Haptodus* and Sphenacodontidae, the comparisons are expanded to include as comparison outgroups the varanopseid *Varanops* and the ophiacodontids, the only other non-therapsid eupelycosaurs in which the carpus and tarsus are well known**.** Unless stated otherwise, comparisons with the carpus and tarsus in *Dimetrodon* rely on descriptions of the former structure by Case (1904), Gilmore (1919), and Romer and Price (1940) and the latter by Romer and Price (1940) and Berman et al. (2004), whereas Romer and Price (1940), Currie (1977, 1979), and Reisz (1986) are the basis for descriptions of both structures in ophiacodontids, *Varanops*, and *Haptodus*.

Although the carpus in *Sphenacodon ferox* is similar in general morphology to those in *Haptodus* and *Dimetrodon*, specific differences are immediately noticeable. The ulnare in *S. ferox* is unique among the non-therapsid eupelycosaurs in its proximal half being greatly flared medially into a broadly convex margin and the distal half being rectangular in outline and lacking an expanded base. The lateral centrale in *Dimetrodon* has a greater proximodistal length and more slender outline compared to those in *S. ferox* and *Haptodus*. Although the difference in the lengths is not great, they are in sharp contrast to the short, nearly square-shaped outline of those in ophiacodontids and *Varanops*. In *S. ferox* and *Dimetrodon*, the first distal carpal is very large and subequal in size to the fourth distal carpal and L-shaped in outline. This element is incompletely known in adult *Haptodus*, although Currie's (1979) reconstruction of the manus in *H. baylei* depicts it as being L-shaped and nearly equal in size to the fourth. In ophiacodontids and *Varanops* the first distal carpal is small to modestly developed, being broad and short in the former and blocky in the latter and therefore lacking an L-shaped outline in both taxa. Currie (1979) observed that in *Haptodus* and *Dimetrodon* the third distal carpal articulates with both the lateral and medial centrale, whereas in ophiacodontids and *Varanops* the third distal carpal articulates proximally with only the lateral centrale; *Sphenacodon ferox* exhibits the former pattern.

The tarsus of *Sphenacodon ferox* closely resembles that of *Dimetrodon*, with *Haptodus* exhibiting a greater similarity to them than to ophiacodontids and *Varanops*. In *S. ferox*, *Dimetrodon*, and *Haptodus* the proximodistally-sloping proximal margin of the astragalus and the free, convex proximomedial corner of the calcaneum join in a near right angle to form the articular surface for the fibula. This is in strong contrast to ophiacodontids and *Varanops* where these margins form a very open, obtuse-angled articulation surface for the fibula. In *S. ferox*, *Dimetrodon*, and *Haptodus* the transverse width of the horizontal arm of the L-shaped astragalus, measured along the distal margin of the astragalus, is much shorter than the proximodistal length of the vertical arm, measured along the lateral margin of the astragalus, which is in contrast to the condition in ophiacodontids and *Varanops* where the two arms are subequal in length. Although in *S. ferox* the transverse width of the horizontal arm is short, it is not quite as reduced as it is in *Haptodus* and *Dimetrodon*. Whereas in *S. ferox* the transverse width of the distal end of the astragalus is 63% of the proximodistal length, the same measurements in *Haptodus* and *D. teutonis* are about 50% and 53%, respectively. The proximodistal length of the calcaneum in *S. ferox*, *Dimetrodon*, and *Haptodus* is greater than the transverse width, whereas the reverse condition is seen in ophiacodontids, especially in

Ophiacodon and *Varanops*, where the calcaneum is greatly flared laterally. The foramen for the perforating artery in *S. ferox* and *Dimetrodon* lies more proximally than in *Haptodus*, ophiacodontids, and *Varanops*, where it is positioned very near the distal end of the astragalus-calcaneum contact.

A massive, transversely broad, L-shaped first distal tarsal with a correspondingly wide proximal end of the first metatarsal occurs in *Sphenacodon ferox* and *Dimetrodon*, though *D. teutonis* appears to be an exception in having a massive, rectangular first distal tarsal with a proximodistal length that is greater than the transverse width. On the other hand, in *Haptodus*, ophiacodontids, and *Varanops* the first distal tarsal is small, with an oval to triangular outline. The only structures of the tarsus in *Haptodus* not exhibited by *Sphenacodon* and *Dimetrodon* but are present in ophiacodontids and *Varanops* are the more distal position of the foramen for the perforating artery and the morphology of the first distal tarsal.

Romer and Price (1940) briefly discussed a trend in pelycosaurian-grade synapsids in which the overall width of the proximal tarsals become narrower, while maintaining the spread of the digits, which they reasoned increased the ability of the pes and lower limb bones to freely rotate about their long axes on one another. This involved a narrowing of the astragalus and calcaneum and a concomitant reduction in size and medial displacement of the medial centrale from a position immediately distal to the astragalus and proximal to the first distal tarsal to one medial to the first distal tarsal. Among sphenacodontids and the closely related *Haptodus*, narrowing of the tarsus appears to have culminated in *Dimetrodon*, based on the currently available material. The tarsus in *Sphenacodon ferox* is not as narrow as that in *Dimetrodon*, or even *Haptodus*, but is definitely narrower than those in ophiacodontids and *Varanops*. Furthermore, the medial centrale in *S. ferox*, as well as that in *Haptodus*, has shifted to the medial side of the first distal tarsal.

In summary, study and comparison of the carpus and tarsus *of Sphenacodon ferox* has revealed trends in their evolution among pelycosaurian-grade synaspids, which are in accordance with recently proposed synaspid phylogenies (Reisz et al., 1992; Berman et al., 1995). That is, the carpus and tarsus in *Haptodus*, *S. ferox*, and *Dimetrodon* appear to exhibit progressively more derived states.

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